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The effects of sterile males and two braconid parasitoids, *Fopius arisanus* (Sonan) and *Diachasmimorpha krausii* (Fullaway) (Hymenoptera), on caged populations of Mediterranean fruit flies, *Ceratitis capitata* (Wied.) (Diptera: Tephritidae) at various sites in Guatemala

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Abstract

Area-wide control of the Mediterranean fruit fly (=medfly), *Ceratitis capitata* (Wiedemann), typically involves sterile insect technique (=SIT), and at present the "Temperature Sensitive Lethal" (=TSL) strain is commonly mass-reared for such releases. In theory, and with some experimental support, the augmentative addition of parasitoids to sterile releases can suppress pest populations to a greater extent than either technique alone. The efficacies of TSL males, parasitoids, and TSL males and parasitoids were compared in large field cages erected over coffee grown at four locations and three altitudes (relatively high, medium and low for the crop) in Guatemala. Two species of opiine braconid parasitoids, the larval–pupal parasitoid *Diachasmimorpha krausii* (Fullaway) and the egg-pupal parasitoid *Fopius arisanus* (Sonan), were released either together or in combination with sterile males into cages along with fertile medflies. Results of this evaluation were assessed by comparing the number of pupae and adult insects that completed development (F1 generation) as a result of the reproduction of a parental generation released into each field cage. The TSL males significantly suppressed F1 fly populations but only in one of four study sites. However, the inclusion of *F. arisanus* and *D. krausii* always provided significant suppression and the effect was frequently substantial. In one site there was a significant interaction between the capacity of sterile males and parasitoids to suppress caged fly populations. There was no effect of host-fruit abundance on the numbers of flies recovered, however, there were significant interactions between maximum and minimum temperatures and the effects of sterile males and parasitoids, respectively. The results suggest that mass-reared sterile medflies and biological control agents should be tested for both consistent sexual-quality and their ability to perform in the various environments in which they will be released.

Keywords: Braconidae; Augmentative release; Sterile insect technique; Mass rearing; Field-cages

1. Introduction

The Mediterranean fruit fly (=medfly), *Ceratitis capitata* (Wiedemann.), is a destructive pest of over 250 species of

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fruits and vegetables (Liquido et al., 1990). In addition to crop losses, it is responsible for the establishment of quarantines that prevent or hinder the development of agricultural exports wherever it occurs. There would be serious economic consequences should the medfly become established in the continental United States. A University of California study estimated a $1.1 billion annual impact to California's economy due to trade embargos, loss of jobs, increased pesticide use, and direct crop losses (Siebert and Pradhan, 1991). At this time, prophylactic treatments of the Los Angeles Basin alone cost $15.4 million annually (Siebert and Cooper, 1995). The 1997–1998 campaign to eradicate medfly from the Tampa, Florida area cost >$ 20 million (Florida Department of Agriculture and Customer Affairs, internal documents).

The medfly is widely distributed across the tropics and subtropics (White and Elson-Harris, 1992). It became established in Hawaii near the turn of the century, and has been periodically introduced, and subsequently eradicated, in California, Florida, and Texas (Clark et al., 1996). At one time, incipient populations were detected in southeastern Mexico, but these were eradicated in the 1970–1980s through the use of insecticide-bait sprays and the Sterile Insect Technique (SIT) (Hendrichs et al., 1983). However, dense populations persist throughout Central America and much of South America, particularly in the vast plantings of coffee, *Coffea arabica* L., in the highlands of Guatemala. The northward spread of medfly into Mexico, and ultimately into the United States, has been prevented by an SIT/insecticide-bait spray barrier maintained along the Mexican/Guatemalan border by the international organization MOSCAMED (United States, Mexico, and Guatemala). Recently, this barrier has been expanded and the possibility of regional eradication of the medfly is under consideration.

In a region-wide eradication program, medfly must be attacked in a variety of environments that may not be amenable to repeated applications of insecticide-bait sprays, such as organic growing areas, urban/suburban locations, and national parks. Under these conditions, it will be important to maximize the impact of the non-chemical, biological components of the control measures, SIT and natural enemies. In addition to the familiar use of SIT to control medfly, there is accumulating evidence that augmentative/innundative parasitoid releases may be an efficacious means of suppressing fruit fly populations (e.g., Sivinski et al., 1996). Furthermore, there are both theoretical reasons and empirical evidence that the combination of SIT and parasitoids can have a synergistic effect and that the two control tactics together would be more efficacious than either one alone (Barclay, 1987; Wong et al., 1992). However, further evaluations are required to document the efficacy of biological agents prior to the introduction of this technology to action programs.

Several species of opiine braconid parasitoids have been mass-reared and augmentatively released against both medfly and pest *Anastrepha* species, and under the best of circumstances have lowered tephritid populations by as much as 95% (e.g., Sivinski et al., 1996). However, there have been lesser results (e.g., Sivinski et al., 2000a), and one reason may be that not all parasitoid species are equally effective under all likely conditions. For example, the braconids attacking *Anastrepha* spp. in Mexico have distinct distributions along an altitudinal gradient that presumably reflect different preferences for temperature and/or moisture (Sivinski et al., 2000b). The altitudinal range of a single host plant, like coffee, can span more than 1000 m in Guatemala and biological control agents released throughout the area must deal with considerable differences in weather and host density. In the same vein, there is little comparative evidence that sterile males of a particular strain perform equally well in the various circumstances they encounter when released across a regional scale. Yet such variability in performance is a possibility. For example, in one set of experiments sterile males of the Temperature Sensitive Lethal (=TSL) strain of *C. capitata* were relatively more likely to mate at a low altitude site in Guatemala than at a higher site (Shelly et al., 2003).

To examine the efficacy of both sterile males and two species of braconid parasitoids at different sites in Guatemala, we placed the various control agents in different combinations into large field cages containing fruiting coffee and fertile medflies. Sterile males were from the TSL strain, a recently developed "sexing-strain" that has been widely used in Guatemala and tested elsewhere. The parasitoids were *Fopius arisanus* (Sonan) and *Diachasmimorpha krausii* (Fullaway). The first species is historically known to be an efficacious egg-prepupal parasitoid (Bess et al., 1961), and the second a relatively little known larval–prepupal parasitoid (Wharton and Gilstrap, 1983). Based on Barclay (1987), we postulated that a combination of species attacking different stages of the host might result in the ultimate destruction of immature flies that escaped earlier parasitism.

2. Methods

2.1. Parasitoids tested

Fopius arisanus occurs naturally from southern India to Taiwan and was first discovered attacking the Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Wharton and Gilstrap, 1983). It was established in Hawaii nearly 50 years ago, and has been subsequently and successfully introduced into Australia, Fiji, and Mauritius. There have been several attempts to introduce it into the Americas: Mexico (1954), Costa Rica (1955), Peru (1960), Argentina (1961), and Florida, USA (1975) (Ovruski et al., 2000). It is only known to have become established in Costa Rica where it has a spotty distribution, and in the only published survey of its abundance, parasitized ~2.5% of the medflies sampled (Wharton et al., 1981). This is in contrast to its performance in Hawaii where it was credited with lowering some medfly populations by 50% and certain Oriental fruit fly populations by 90% (Bess et al., 1961; see also Vargas et al., 2001). This

disparity between Hawaii and Latin America may be due to the lack of suitable alternative tephritid hosts in the neotropics. Although *F. arisanus* develops in all of the *Anastrepha* spp. so far examined, (Jorge Cancino; pers. communication), it tends to do so at a much lower rate than it does in Oriental fruit fly or even medfly. In Costa Rica, it was only recovered from <1% of an *Anastrepha* sp. infesting *Psidium guajava* L. (Wharton et al., 1981).

Diachasmimorpha krausii was originally recovered from *Bactrocera* sp. in the Indo-Australian region (Wharton and Gilstrap, 1983). It was introduced into Hawaii in 1950, but failed to become established. *Diachasmimorpha krausii* has been reared for some years in the USDA-APHIS/MOSCAMED "La Aurora" facility in Guatemala City and because of preliminary field releases in Guatemala was considered a relatively promising candidate for augmentative/innundative release by the authors. The fecundity and longevity of both it and *F. arisanus* are unaffected by exposure to the low temperatures associated with chilling prior to aerial release (Baeza et al., 2002).

2.2. Sources of insects

Sterile TSL and fertile "bisexual-Antigua strain" medflies were obtained from the MOSCAMED mass-rearing facilities at El Pino and La Aurora, Guatemala, respectively. The Antigua-strain had been long domesticated and was used in lieu of wild flies largely for logistical reasons; i.e., sufficient numbers of wild flies were not easily available. We appreciate that Antigua-strain females may exercise less mate choice than wild females (e.g., Lance et al., 2000), and that this would overestimate the efficacy of sterile males in our experiments. As a result relative comparisons with parasitoid efficacies would be conservative. TSL sterile males were 5-day old at the time of introduction into the field cages, while fertile insects were 7-day old. Fertile flies had been separated by sex within 24 h of emergence and were virgins when introduced at a sex ratio of 1:1 into the cages. *Fopius arisanus* had been in colony at the MOSCAMED Aurora rearing facility in Guatemala City for 3 years and *D. krausii* for 4 years. At the time of introduction into the cages, *F. arisanus* were 10-day old and *D. krausii* 6-day old.

Diachasmimorpha krausii was originally obtained from R. Messing of the University of Hawaii and *F. arisanus* was obtained from colonies initiated by E. Harris at the USDA-ARS facility in Honolulu, Hawaii. Rearing methods were similar to those described by Harris and Okamoto (1991) and Wong and Ramadan (1992). TSL males had been sterilized as pupae ca. 48 h prior to eclosion through exposure to 100 Gy (central target dose) of gamma radiation at the El Pino MOSCAMED facility.

2.3. Experimental locations

All sites were commercial coffee plantations planted with the "Bourbon" cultivar, with the exception of Finca Sabana Grande which grew a mixture of "Bourbon" and "Catuai." At all the sites the bushes were ~2–2.5 m in height and grown under the canopies of various shade trees. None of the shade trees were included among the caged vegetation. The sites were chosen on the basis of their various altitudes and represent a diversity of local coffee growing environments. In order of altitude the sites were: (1) Santa Anita (340 m; N14E 24′ 14.0″, W91E09′ 09.1″); (2) Sabana Grande (670 m; N14E 21′56.7″, W90E49′40.4″); (3) Santa Alicia (1540 m; N14 E36′54.1″, W91E09′00.4″) and (4) Retana (1560 m; N14E33′13.3″ W90E45′06.6″). Mean temperatures (Standard Errors), maximum and minimum temperatures were measured by hygrothermigraph throughout the duration of the experiments (Table 1). In a similar region in southern Mexico altitude is positively correlated to rainfall and negatively related to temperature (Table 1; Sivinski et al., 2000b).While the number of caged coffee bushes, 15/replicate, was the same at all sites, there were different amounts of coffee fruits collected at each (Table 2).

Table 1
The periods of time in which adult sterile TSL strain Mediterranean fruit fly and the parasitoids *Fopius arisanus* and *Diachasmimorpha krausii* were present in the field cages and the mean (standard error), maximum, and minimum temperatures (°C) recorded during that period

Site	Dates	Mean temperature	Maximum temperature	Minimum temperature
Santa Anita	10/29–11/15	23.8 (4.2)	35.6	17.5
Sabana Grande	12/19–1/17	22.8 (3.7)	36.4	13.2
Retana	1/23–2/24	17.3 (5.6)	33.2	3.7
Santa Alicia	1/29–2/28	16.8 (6.0)	37.9	14.2

Table 2
The mean (SE) weight (kg) of coffee berries harvested following exposure to the various field cage treatments

Treatment	Santa Anita	Sabana Grande	Retana	Santa Alicia
Sterile− Parasitoids−	9.4 (1.9)	24.7 (2.3)	18.7 (3.2)	13.1 (1.6)
Sterile+ Parasitoid−	8.6 (1.3)	15.0 (3.4)	19.6 (1.1)	17.8 (3.2)
Sterile+ Parasitoid+	7.7 (0.5)	12.4 (2.6)	17.7 (1.8)	11.8 (1.5)
Sterile− Parasitoid+	8.0 (0.7)	14.9 (1.7)	21.8 (4.3)	17.1 (0.9)

Sites are listed by increasing altitude; S, sterile TSL strain Mediterranean fruit flies, *Fa*, *Fopius arisanus*, *Dk*, *Diachasmimorpha krausii*.

2.4. Field cages

The eight field cages simultaneously placed at each site were 15 m × 6.4 m and 2.4 m high. They had no floors, but the entrance and exit of insects along the bottom margins were prevented by the burial of the edges in soil. Once erected, the cages were divided into two equal portions by a canvas barrier secured to the walls and ceiling with velcro strips. Treatments were randomly assigned to the various cage sections. A 1:1 solution of water and honey was provided in ~30 cm plastic tubes, sealed at each end with cotton wicks and attached to each of the bushes.

2.5. Schedule of control agent introduction

The treatments consisted of sterile flies alone, and various combinations of parasitoids with and without sterile flies (Table 3). There were 4 replicates of each treatment per each of the 4 sites. TSL males were released at the ratio of 100 sterile flies: 1 fertile female fly with an adjustment made for emergence and flight ability. Females of each parasitoid species were released at rates of 10 parasitoid: 1 fertile female fly (=1/10 of the release rate of sterile flies). Because the stage at which the egg-pupal parasitoid (*F. arisanus*) and sterile flies effect control differed from that of the larval–pupal parasitoid (*D. krausii*), the agents were introduced into the cages at different times. The timing of the introduction of *D. krausii* was determined by the maturation of larvae in separate and smaller "sentinel" field cages covering single coffee bushes and located near the larger experimental "test" cages. Because fly larvae developed at different rates at the various sites, presumably due to temperature differences, the timing of *D. krausii* introduction following the introduction of the flies also varied.

2.6. Recovery and handling of pupae

Coffee berries inside the "test" and "sentinel" cages had originally various states of ripeness. Coffee berries inside "sentinel" cages were surveyed/harvested weekly as they ripened over a period of three weeks. Once it was determined from these surveys that a high percentage of larvae was about to reach the 3rd instar (prior to leaving fruit and "jumping"), all of the coffee berries within each "test" cage at a particular site were picked on the same day. Berries from individual bushes were weighed and kept separately in plastic sieves placed over plastic buckets containing dampened sawdust. Every 2 days, the sawdust was sifted, and the pupae counted and put aside for subsequent adult emergence. Each container had at least four larval/pupal collections. The berries were then examined individually for larvae and pupae that had failed to leave to the sieve and make their way into the bucket. Pupae were held for a period of at least 30 days and the adult insects were identified and sexed. Unemerged puparia were then dissected to determine if they contained either a dead fly or parasitoid.

Table 3
The numbers and combinations of insects added to the various field cages. *F*, fertile female "standard" strain Mediterranean fruit fly; *S*, sterile male TSL Mediterranean fruit flies; *Fa*, female *Fopius arisanus*; *Dk*, female *Diachasmimorpha krausii*

Treatment	*F*	*S*	*Fa*	*Dk*
Sterile− Parasitoid−	110			
Sterile+ Parasitoid−	110	11,000		
Sterile+ Parasitoid−	110	11,000	1100	1100
Sterile− Parasitoid+	110		1100	1100

In all cages where female parasitoids or fertile medflies were released, equal numbers of males were also added.

2.6.1. Data analysis

Among untreated controls there were no significant correlations between the amounts of coffee fruits in a cage and the resulting numbers of *C. capitata* pupae or adults (r[fruit weight × pupae] = 0.099, $n = 16$, $p = 0.74$; r[fruit weight × adults] = 0.89, $n = 16$, $p = 0.74$). This might suggest that the caged fly populations were not resource limited and that the actual numbers of flies should be used in analyses as opposed to a resource-relative measurement such as flies/kg of fruit. However, *F. arisanus* is known to inflict considerable egg mortality (Harris and Bautista, 2001), and it is difficult to extrapolate the extent of any competition among flies for oviposition sites from the numbers of their pupae and adults. As a result the effects of the various treatments on both the actual numbers and relative numbers of adults and pupae are displayed graphically. Quantitative results are presented for flies/kg, but in instances where the use of actual fly numbers yields a significantly different outcome these results are mentioned as well. Because the numbers of adult flies recovered reflected all the sources of mortality introduced into the cages (egg mortality due to failed oviposition, larval and pupal mortality due to failed parasitism, and parasitism) adult fly numbers rather than numbers of pupae were considered in subsequent analyses.

The effects of sterile male flies and the parasitoids *Diachasmimorpha krausii* and *Fopius arisanus* on the numbers of adult *C. capitata*/kg of coffee fruits were determined through a factorial analysis of variance where the 4 treatments were: (A) no sterile flies and no parasitoids, (B) sterile flies and no parasitoids, (C) sterile flies and both parasitoids, and (D) no sterile flies but both parasitoids (proc GLM; SAS Inst., 1989). Initial analyses considered each site independently, but all sites were combined to examine the effects of that differed among sites, mean temperature and host-fruit densities (differed among cages). Their relationships to the effects of either sterile males or parasitoids were examined through interaction effects.

3. Results

Two measures of *C. capitata* reproduction within the field cages, the numbers of pupae harvested and the number of adult flies emerged, were available for comparison

among treatments. Both are presented in Fig. 1, but because mortality due to the larval–prepupal parasitoid *D. krausii* is not fully reflected in the numbers of pupae recovered, analysis of treatment effects concentrated on adult flies/kg of coffee fruits. The mean numbers of adult flies recovered independent of the amount of coffee fruits in the cages are presented in Fig. 2.

At sites 1, 2, and 3, parasitoids, but not sterile flies, had a significant effect on the numbers of adult flies recovered. There were no interaction effects. At site 4, both sterile flies and parasitoids had a significant effect on the numbers of adult flies emerged and there was a significant interaction effect (Table 4). When mean fly numbers independent of coffee berry abundance was considered parasitoids were as before, but sterile releases had an effect at both sites 3 and 4 ($F(\text{site } 3) = 5.0$; $df = 1, 12$; $p < 0.05$; $F(\text{site } 4) = 26.0$; $df = 1, 12$; $p = 0.0003$). Again, at site 4 there was a significant interaction between sterile males and parasitoids ($F = 20.3$; $df = 1, 12$; $p = 0.0007$).

While parasitoids were effective at all sites, what might account for the difference among the sites in the control provided by sterile flies? One possibility is environmental factors. Distributions of both fruit flies and their parasitoids are influenced by altitude (Sivinski et al., 2000a, 2004), which presumably is due in turn to temperature and moisture gradients. Mean temperatures among sites had a significant interaction effect with both sterile flies and parasitoids ($F(\text{sterile flies}) = 7.17$; $df = 1, 56$; $p = 0.03$; $F(\text{parasitoids}) = 5.19$; $df = 1, 56$; $p < 0.001$). However, when actual numbers of flies are considered mean temperature had a significant interaction only with the effects of parasitoids ($F(\text{parasitoids}) = 20.6$; $df = 1, 56$; $p < 0.001$). Sterile males appear to have performed better at warmer maximum temperatures and parasitoids relatively well at lower minimum temperatures. Cages differed not only in temperature at the various sites, but also in the numbers of fruit present in each, and host distribution could influence parasitoid foraging behavior (Bellows and Hassell, 1999). However, there was no significant interaction between the effects of either sterile flies or parasitoids on adult fly emergence and the numbers of fruit present.

Parasitism rates (number of parasitoids/number of parasitoids + number of adult *C. capitata*) in the various cages ranged from 6 to 55% (Table 5). However, the mortality

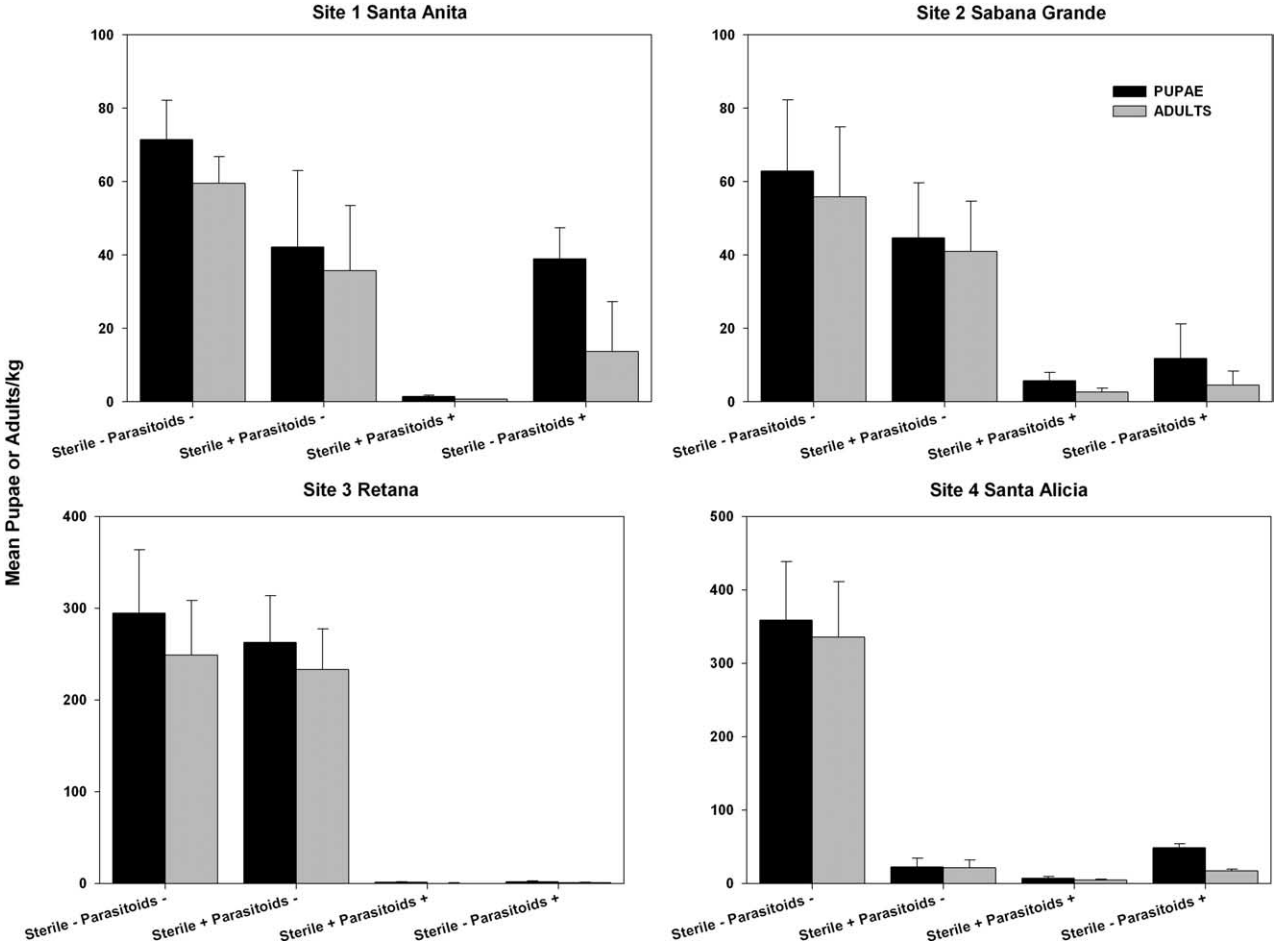

Fig. 1. The mean (±standard error) numbers of Mediterranean fruit fly puparia and adult flies/kg of coffee fruits recovered from field cages containing fertile flies and various combinations of sterile males and parasitoids.

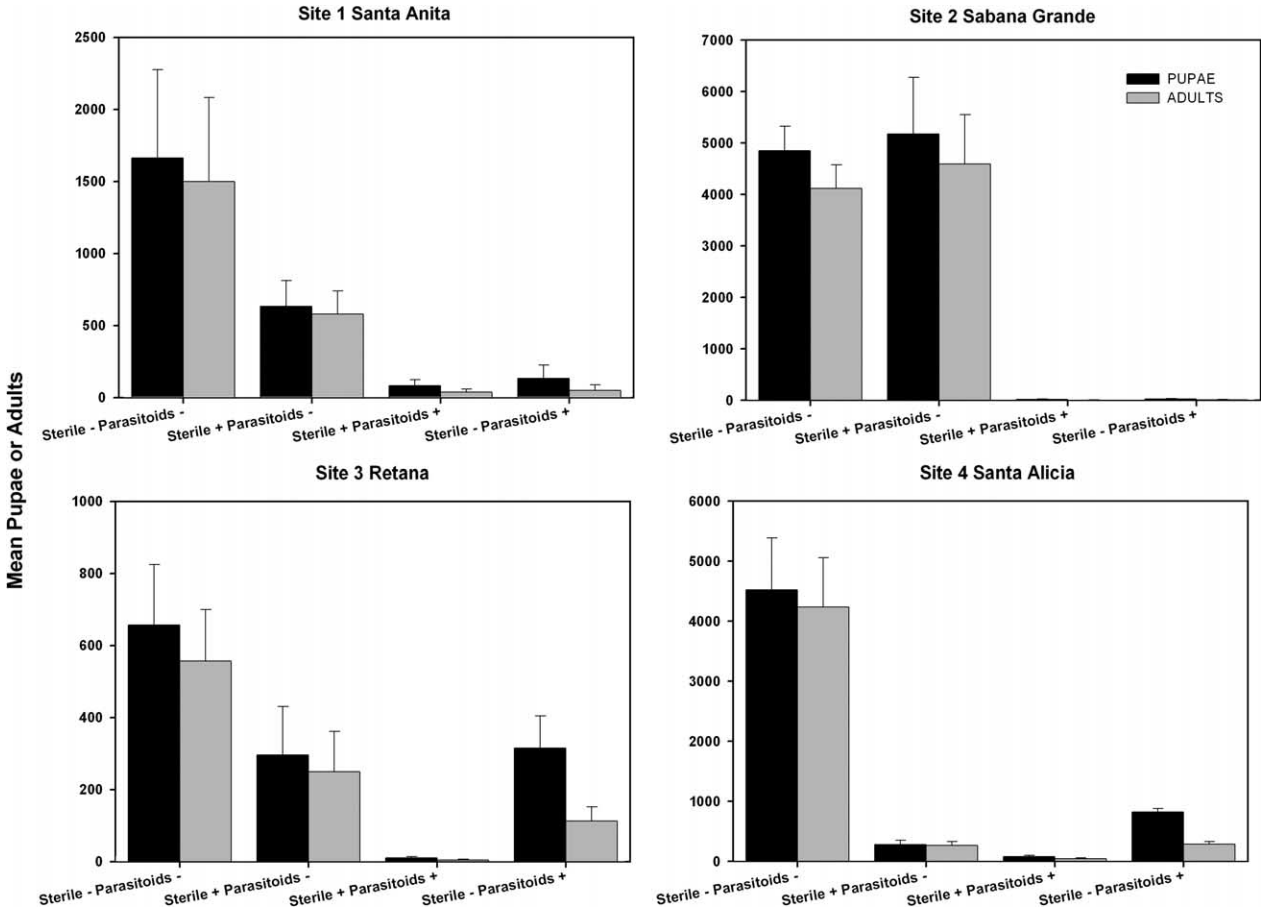

Fig. 2. The means (±standard error) of the actual numbers of Mediterranean fruit fly puparia and adult flies recovered from field cages containing fertile flies and various combinations of sterile males and parasitoids.

Table 4
ANOVA table for the effects of sterile flies, parasitoids and their interaction on the numbers of adult Mediterranean fruit fly recovered from field cages in each of four experimental sites

	MS	*F*	*p*
Site 1			
Sterile	283.6	0.5	0.49
Parasitoid	8022.6	14.1	0.003
Sterile * parasitoid	168.5	0.3	0.60
Site 2			
Sterile	246.3	0.04	0.84
Parasitoid	230968.1	41.6	< 0.0001
Sterile * parasitoid	229.8	0.00	0.84
Site 3			
Sterile	1350.9	3.52	0.09
Parasitoid	6549.7	17.1	0.001
Sterile * parasitoid	115.8	0.3	0.59
Site 4			
Sterile	107354.2	18.4	0.001
Parasitoid	112343.7	19.3	0.0009
Sterile * parasitoid	91236.8	15.7	0.002

$df = 1, 12$.

inflicted by the parasitoids was more apparent in the depressed number of pupae and emerging adults than in the parasitism rates.

4. Discussion

This set of field cage experiments yielded three results of interest to those involved with fruit fly management: (1) augmented parasitoids, particularly *Fopius arisanus*, are a potentially efficacious control of *C. capitata* under a variety of conditions in Guatemala; (2) the combination of parasitoids and sterile flies sometimes resulted in increased effectiveness; and (3) neither parasitoids nor sterile males of the TSL strain were equally effective in all temperature-environments.

Inclusion of *F. arisanus*, and *D. krausii*, always resulted in significant control and the suppression was frequently dramatic. Although we had anticipated that the combination of egg and larval parasitoids might render immature flies vulnerable to attack over a longer period of time and so be particularly effective, it appears that the mortality caused by parasitoids was due largely to unsuccessful oviposition attempts by *F. arisanus* that resulted in failure of the host egg to develop (e.g., Harris and Bautista, 2001). Tephritid eggs are near the fruit surface and more accessible to parasitoids than larvae feeding deeply in the pulp (Sivinski and Aluja, 2003). In addition, oviposition into the relatively small and fragile egg may damage the host embryo and substantial egg mortality has been inflicted

Table 5
Mean (SE) parasitism rates (parasitoids/parasitoids + Mediterranean fruit flies) resulting from the various combinations of biological control agents in the different sites: *Fa*, *Fopius arisanus*, *Dk*, *Diachasmimorpha krausii*

Treatment	Parasitism	Santa Anita	Sabana Grande	Retana	Santa Alicia
Sterile+ Parasitoid+	Total	.06 (.03)	.43 (.08)	.31 (.07)	.29 (.10)
	Fa	.06 (.03)	.23 (.07)	.27 (.08)	.23 (.08)
	Dk	0	.20 (.02)	.04 (.04)	.06 (.02)
Sterile− Parasitoid+	Total	.34 (.06)	.55 (.02)	.19 (.07)	.45 (.05)
	Fa	.14 (.05)	.38 (.07)	.14 (.06)	.35 (.07)
	Dk	.20 (.04)	.17 (.06)	.05 (.03)	.11 (.02)

by *F. arisanus* in Hawaiian Mediterranean and oriental fruit fly populations (Bess et al., 1961). Since *D. krausii* attacks late-instar larvae, its significant contribution to mortality might be expected to take the form of large numbers of the parasitoid emerging from large numbers of host puparia. This was never the case, and more *F. arisanus* than *D. krausii* adults were recovered in 7 of the 8 instances when the two species were present in the same field cages. It seems likely that *D. krausii* simply had few hosts to attack and so had little impact overall.

Sterile males alone significantly suppressed the caged fly populations only at the Santa Alicia site. This may have been due to a particularly favorable environment or a particularly competitive cohort of TSL sterile males. Previous studies had suggested that TSL flies were least efficacious at high altitudes (Shelly et al., 2003), but in the present experiments sterile males were both significant and insignificant in their effects on *C. capitata* numbers at the highest altitude sites (sterile males were effective at both high altitude sites when actual numbers of flies recovered are considered).

Another potential source of variance in the effect of the sterile males was inconsistent quality of the flies. If this was the sole cause of variance, it meant that relatively poor quality flies were obtained on three separate occasions and that only once did the sterile males reach their sexual potential and provide a significant level of control.

Given the substantial investment in fruit fly SIT there has been surprisingly little investigation into the environmental preferences and limitations of various mass-reared strains. The use of genetic sexing strains (GSS) is clearly a step forward in SIT technology. However, further improvements in this technology are required to secure eradication and maintain fly-free areas. The inconsistent performance of the TSL strain, due either to environmental or production variability, in the present experiment and in the study of Shelly et al. (2003), suggests that control programs would benefit from becoming thoroughly acquainted with the characteristics of the flies being mass-reared, consider maintaining various strains with different genetic qualities, and possibly even applying the most appropriate strain for any particular set of circumstances.

In addition to increased awareness of possible variance in the quality of the sterile males, future SIT experiments such as this might benefit from the use of wild-type medflies as the parental generation within the field cages. It is possible that mass reared-strain females might be either less or more likely to mate with sterile males than their wild counterparts (e.g., Cayol et al., 1999). Of these possibilities the most likely is that domestic females are less choosey than wild females (Lance et al., 2000). If so, the present results over estimate the efficacy of sterile males and suggest an even more important role for parasitoids.

While parasitoids and their combination have offer potential benefits, mass-rearing of many species of fruit fly parasitoids is still relatively expensive and this could limit their adoption. The development of more efficient rearing techniques requires additional attention, and we believe that promising results such as reported here may focus attention on solutions to these problems. The same research and quality control procedures recommended to assess sterile insects should also be applied to parasitoids destined for augmentative/inundative release, and to date some progress has been made toward this goal with the natural enemies of pest species of *Anastrepha* in Mexico (e.g., Lopez et al., 1999; Sivinski et al., 1997, 2000b). These studies are examples of what might be undertaken with Mediterranean fruit fly parasitoids, and indicate that various species have clear habitat preferences on scales ranging from the regional to within fruit tree canopies. Microhabitat preferences may lead area-wide parasitoid augmentation/inundation programs to release multiple species, each capable of best exploiting a particular portion of the heterogeneous environments within and surrounding agroecosystems.

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